

# 苹果砧木资源评价与利用研究进展

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**摘要:** 优良砧木选用是苹果生长发育和优质高效生产的基础。砧木不仅影响苹果的树形、抗逆性和适应性, 还影响其产量和品质。我国是苹果属植物的重要起源地之一, 拥有大量的抗性种质资源, 充分挖掘和利用丰富的苹果资源, 对苹果产业高质量发展具有十分重要的意义。对苹果砧木资源在非生物逆境(干旱、盐碱、寒害、涝害和缺素等)胁迫下的抗性评价以及矮化砧木选育和利用等方面进行综述, 并对我国苹果砧木资源研究和利用中存在的问题进行分析和讨论, 以期为苹果砧木的选择和利用提供理论依据。

**关键词:** 苹果; 砧木; 抗逆性; 矮化; 评价与利用

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## Research advances in the evaluation and utilization of apple rootstock germplasm

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**Abstract:** Apple (*Malus × domestica* Borkh.) is one of the major cultivated fruit crops in China, and its cultivation area and yield rank first globally. The selection of excellent rootstock varieties is the basis and guarantee for high quality and high yield of apple. Rootstock affects not only its stress resistance and adaptability, but also the quality and yield of apple. In recent years, abiotic stressors, such as drought, soil salinity, heat and cold, are major limiting factors, which result in a decline in fruit quality and yield of apple, and seriously affect the healthy and sustainable development of the apple industry. These threats are likely to become even more significant under climate change and the pressures of an ever-growing human population. The stress resistance of apple trees mainly depends on the rootstock. Therefore, it is of great significance for the development of apple industry to identify and evaluate the resources of apple rootstock and screen the excellent rootstocks with strong stress resistance. China is one of the world's largest apple origin centers, abundant in germplasm resources, and holds great potential for resource innovation and utilization. It is of utmost significance for the development of the apple industry to select outstanding rootstocks with strong stress resistance and dwarfing traits. In this paper, the research and utilization situation of apple rootstock resources both at home and abroad was reviewed to provide a basis for the breeding and wide application of apple rootstocks. The main results are as follows: (1) Apple belongs to Rosaceae family, which comprises 36 species in the world, of which 25 are native to China, including more than 100 variant types. Among these different species and types, there are abundant resources of apple rootstocks with utilization and potential utilization value, which have excellent germplasm such as drought resistance, cold resistance, flood resistance, salt toler-

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ance, iron deficiency resistance and apomixis. Some of these rootstocks are directly used in production. For a long time, *M. sieversii*, *M. robusta*, *M. hupehensis* and *M. baccata* have been used as rootstocks in most apple producing areas in China. (2) Apple often suffers from adverse stresses, such as drought, low temperature, salt and alkali, which affects its growth and development and reduces its yield and fruit quality. It has been found that the drought tolerance of *M. sieversii*, *M. prunifolia* and *M. toringoides* are strong. The salt tolerance of apple rootstock varies greatly among different species, ecotypes and even among different individuals, and the salt tolerance of *M. xiaojinensis* and *M. prunifolia* were strong. Cold damage often occurs in many apple producing areas in north China, which threatens the development of apple production, so the evaluation on cold resistance of apple rootstock, breeding of cold resistant rootstock and the study on cold resistance mechanism have attracted much attention. In terms of cold resistance evaluation, membrane permeability, relative water content and malondialdehyde are considered to be closely related to cold resistance. GM256 and CX3 are two apple rootstocks that have been reported to be cold-resistant in China. (3) Dwarf cultivation is the development trend of apple production in the world, and dwarf rootstock is one of the main ways to achieve dwarf density-planting. Some dwarfing rootstocks, including SH series, Liaozen, GM256 and Qingzhen, were bred by hybridization with apple resources in many agricultural institutions in our country. At present, dwarfing rootstocks used in apple production in China mainly include M9T337, M26, MM106, B9, SH, GM256 and so on. (4) In the past two decades, the cultivation mode of apple in the world has undergone fundamental changes, the tree shape is developing from standard planting to dwarf dense planting, and management is developing from time-consuming and labor-intensive to labor-saving. At present, in the United States, Italy, New Zealand and other countries, the dwarf cultivation has accounted for more than 70% of the total area of apple cultivation. However, 80% of apple trees in China are still applying standard planting. Standard-planting apple trees have large crowns, poor light reception, inferior fruit quality, and the cultivation and management costs are high, in which the labor cost has accounted for more than 60% of the total cost of apple production. The stress resistance and tree shape of the apple depend mainly on the rootstock. Under the new situation, how to cultivate and create apple rootstock that is resistant to stress and suitable for labor-saving cultivation and management has become a key scientific problem to be solved urgently in apple cultivation and management in China. (5) Although some apple germplasm resources such as *M. sieversii*, *M. prunifolia* and so on have strong drought resistance, they are vigorous. *M. hupehensis* has the characteristics of apomixis, but its drought resistance is poor and it is vigorous. In addition, the scion varieties on the seedling rootstock have some problems such as delaying fruit maturity. At present, there is a lack of apple rootstock varieties with good comprehensive traits like strong resistance and dwarfing. How to scientifically develop, breed and utilize these excellent germplasm resources is an important topic in the present research. (6) With the rapid development of molecular biology and genomics of fruit crops, people are shifting the research focus of apple rootstock from physiological traits to genetic mechanism. The completion of whole genome sequencing of apple provides a good genomic data platform for further analysis of important agronomic traits of apple rootstocks. At the same time, it will lay a solid foundation for breeding new varieties of apple rootstock with excellent characteristics such as strong resistance, dwarfing and apomixis. Therefore, accelerating the evaluation, identification, development and utilization of apple wild resources and strengthening the selection and breeding of new apple rootstocks will be of great significance to the healthy, stable and sustainable development of the apple industry in China and even on the world.

**Key words:** Apple; Rootstock; Stress resistance; Dwarf; Identification and evaluation

苹果(*Malus × domestica* Borkh.)是我国主要栽培的果树之一,栽培面积和产量均居世界首位<sup>[1]</sup>。苹果产业在精准扶贫、乡村振兴及生态保护中发挥重要作用。苹果产业的快速发展离不开优良新品种的选育、应用和推广。优良的砧木是苹果优质高效生产的基础和保证,砧木不仅影响苹果植株的适应性和抗逆性,还影响品质和产量<sup>[2-4]</sup>。随着全球变暖,极端气候频繁出现,经常发生大面积、不同程度的干旱、低温、盐碱等非生物胁迫,造成苹果果实品质和产量下降,严重影响苹果产业健康可持续发展<sup>[5-6]</sup>。苹果的抗逆性主要取决于砧木,因此,对苹果砧木资源进行鉴定与评价,筛选抗逆性强并矮化的优良砧木,对苹果产业的发展具有重要意义。笔者就国内外苹果砧木资源的研究和应用现状及抗逆性

研究进行了综述,以期为苹果砧木的选择和利用提供依据。

## 1 苹果砧木资源在非生物胁迫抗性中的评价及利用

据李育农<sup>[7]</sup>报道,苹果有36个种,其中原产于我国的有25个种,包含了100多个变异类型。在这些不同的种及其类型中,蕴藏着丰富的具有抗旱、抗寒、抗涝、耐盐、抗缺铁及矮化、半矮化和无融合生殖等优异的苹果砧木资源,其中有些苹果种质资源可直接应用于生产<sup>[6,8-10]</sup>。长期以来,多位研究者对苹果砧木资源在抗旱、抗寒、耐盐等非生物胁迫中的抗性进行鉴定与评价,挖掘了一批特异种质资源(表1)。

表1 原产我国苹果资源的非生物胁抗性

Table 1 Abiotic stress tolerance of apple germplasm resources in China

品种 Cultivar	学名 Scientific name	耐旱性 Drought tolerance	耐盐性 Salt tolerance	抗寒性 Cold tolerance	耐涝性 Waterlogging tolerance
平邑甜茶	<i>M. hupehensis</i> Rehd.	较弱 Slightly weak <sup>[9,11]</sup>	较强 Slightly strong <sup>[12]</sup>	一般 Average <sup>[13]</sup>	强 Strong <sup>[10,14]</sup>
新疆野苹果	<i>M. sieverii</i> Roem	强 Strong <sup>[11]</sup>	一般 Average <sup>[15]</sup>	较弱 Slightly weak <sup>[13]</sup>	弱 Weak <sup>[10]</sup>
山定子	<i>M. baccata</i> Borkh.	较弱 Slightly weak <sup>[9]</sup>	弱 Weak <sup>[12]</sup>	强 Strong <sup>[13]</sup>	一般 Average <sup>[10]</sup>
八棱海棠	<i>M. robusta</i> Rehd.	一般 Average <sup>[9]</sup>	较强 Slightly strong <sup>[12]</sup>	较强 Slightly strong <sup>[13]</sup>	一般 Average <sup>[10]</sup>
小金海棠	<i>M. xiaojinensis</i>	-	强 Strong <sup>[15-16]</sup>	较强 Slightly strong <sup>[13]</sup>	一般 Average <sup>[17]</sup>
富平楸子	<i>M. prunifolia</i> Borkh.	强 Strong <sup>[12,11]</sup>	较强 Slightly strong <sup>[16]</sup>	-	一般 Average <sup>[10]</sup>
变叶海棠	<i>M. toringoides</i> Hughe	较弱 Slightly weak <sup>[11]</sup>	较弱 Slightly weak <sup>[12]</sup>	较强 Slightly strong <sup>[13]</sup>	弱 Weak <sup>[10]</sup>
垂丝海棠	<i>M. halliana</i> Koehne	较强 Slightly strong <sup>[17]</sup>	较强 Slightly strong <sup>[18]</sup>	-	较强 Slightly strong <sup>[17]</sup>
卢氏红果	<i>M. sieboldii</i> Rehd.	-	较弱 Slightly weak <sup>[16]</sup>	-	较强 Slightly strong <sup>[10,14]</sup>
西府海棠	<i>M. micromalus</i> Hemsl	较强 Slightly strong <sup>[17]</sup>	-	-	一般 Average <sup>[14]</sup>
毛山荆子	<i>M. mansurica</i> Komarov	弱 Weak <sup>[17]</sup>	较弱 Slightly weak <sup>[17]</sup>	较强 Slightly strong <sup>[17]</sup>	一般 Average <sup>[14]</sup>
红三叶海棠	<i>M. sieboldii</i> Rehd.	较弱 Slightly weak <sup>[17]</sup>	弱 Weak <sup>[18]</sup>	-	较弱 Slightly weak <sup>[14]</sup>
平顶海棠	<i>M. robusta</i> Rehd.	-	一般 Average <sup>[15,17]</sup>	-	较强 Slightly strong <sup>[14]</sup>
丽江定子	<i>M. rockii</i> Rehd.	-	弱 Weak <sup>[12]</sup>	弱 Weak <sup>[17]</sup>	较强 Slightly strong <sup>[14]</sup>
崂山柰子	<i>M. prunifolia</i> Mill.	-	一般 Average <sup>[15]</sup>	弱 Weak <sup>[13]</sup>	较弱 Slightly weak <sup>[14]</sup>

注:“-”代表砧木的这种抗性未被报道。

Note: “-”indicates that this resistance of the rootstock has not been reported.

### 1.1 耐旱性

干旱是苹果生产中经常遇到的问题,严重制约苹果产业的发展<sup>[19-20]</sup>。我国是苹果属植物的重要起源地之一,拥有大量的抗旱种质资源,耐旱性较强的种质有新疆野苹果、楸子和东北黄海棠等<sup>[9,21-22]</sup>。研究发现不同种或类型的苹果砧木的抗性差异较大(表1)。叶乃好等<sup>[9]</sup>对10种苹果砧木资源进行了抗旱性鉴定与评价,发现Luo-6、Luo-2是耐旱性强的砧木,八棱海棠,莱芜茶果、黄海棠是中等耐旱砧木,

山定子、平邑甜茶、六蜜海棠为不耐旱砧木。Ma等<sup>[23]</sup>用隶属函数值法对10种苹果砧木的抗旱性进行了综合评价,发现楸子和新疆野苹果耐旱性较强,而平邑甜茶和变叶海棠耐旱性较差。傅明洋<sup>[20]</sup>发现楸子不同类型之间的耐旱性也有显著差异,耐旱性较强的苹果砧木有富平楸子、东北黄海棠;中等抗旱的砧木为吴起楸子、五棱海棠以及崂山柰子;抗旱性相对较弱的是红海棠和白海棠。魏江彤等<sup>[11]</sup>对8份苹果种质资源的抗旱性进行评价,发现LC36和L7

(*M. soulardii*)的耐旱性强于新疆野苹果和楸子。

Wang 等<sup>[24]</sup>比较分析了两种苹果砧木的耐旱性差异机制,发现干旱胁迫下耐旱性强的苹果砧木楸子受到的氧化胁迫伤害较小,且其抗氧化防御能力强于耐旱性较差的平邑甜茶。Tworkoski 等<sup>[25]</sup>对两种无性系苹果砧木 MM111 和 M9 进行了耐旱性比较分析,结果发现,M9 通过提高ABA 含量,增强其耐旱性,而 MM111 则是通过较多的延长根来提高耐旱性。Liu 等<sup>[21]</sup>以抗旱性差异显著的两种苹果砧木楸子和平邑甜茶为材料,研究了中度干旱下两种砧木 6 个水通道蛋白基因表达的变化,发现干旱胁迫下 6 个水通道蛋白基因都上调表达,但苹果砧木间的表达有显著差异,推测这可能是造成两种苹果砧木抗旱性不同的主要原因。

## 1.2 耐盐性

土壤盐碱化是干旱、半干旱及沿海滩涂地区苹果生产栽培的主要障碍<sup>[26]</sup>。苹果砧木的耐盐性在不同苹果种间、不同生态类型间及不同个体间都有较大差异。杜中军等<sup>[12]</sup>通过盆栽对 19 种苹果砧木进行了耐盐性评价,发现 Luo-1、Luo-2 和珠美海棠为高耐盐的苹果砧木,变叶海棠、山定子、丽江山定子、德钦海棠和花红为不耐盐苹果砧木。Yin 等<sup>[16]</sup>通过水培对 15 种苹果砧木的耐盐性进行了综合评价,发现楸子、东北黄海棠、大果红三叶海棠和小金海棠属耐盐性苹果砧木,而卢氏红果、樱叶海棠和西府海棠则属不耐盐苹果砧木。林冰冰等<sup>[15]</sup>对 16 个种 80 份苹果砧木资源 1 年实生苗进行了耐盐性评价分析,发现实施高盐胁迫 10 d 后,盐害指数变异为 0.00~0.90,变异系数为 0%~173%;耐盐性强的种质资源有 7 份,耐盐性较强的 57 份,耐盐性弱的共 16 份。

Molassiotis 等<sup>[27]</sup>以苹果砧木 MM106 为试材,比较研究了 NaCl 和 KCl 处理下的生理生化指标,发现两种氯盐显著抑制植株生长,降低了叶绿素含量、光合效率和矿质元素利用效率。王慧英等<sup>[28]</sup>发现小金海棠和 M7 耐盐性有显著差异,耐盐性较强的小金海棠叶中的  $\text{Na}^+$ 、 $[\text{Na}^+]/[\text{K}^+]$  均小于耐盐性差的 M7,而根中则相反,且耐盐性较强的苹果砧木小金海棠根中  $\text{Na}^+$  增加幅度较大。说明苹果砧木可能的耐盐机制是根系能截留较多的  $\text{Na}^+$ ,并以某种形式阻止部分  $\text{Na}^+$  向地上部的运输,从而减轻了盐离子对地上部的毒害作用。Li 等<sup>[29]</sup>研究发现,盐胁迫下平邑甜茶叶片中离子转运蛋白和水通道蛋白相关基因

*MdHKT1*、*MdSOS1* 和 *MdNHX1* 的表达量显著高于樱叶海棠,说明平邑甜茶具有更强的使  $\text{Na}^+$  外排和将  $\text{Na}^+$  区隔到液泡中的能力,从而提高了耐盐性。薛浩等<sup>[30]</sup>研究了寒富二倍体和同源四倍体苹果的耐盐差异机制,发现盐胁迫下二倍体和同源四倍体苹果中水通道相关蛋白基因 *MdPIP1;1*、*MdPIP2;1*、*MdTIP1;1* 和 *MdTIP2;1* 的表达量都呈先下降后上升高趋势,但四倍体的表达量显著高于二倍体,推测四倍体苹果的耐盐性强可能与水通道蛋白基因的表达水平较高有关。

## 1.3 抗寒性

我国北方的一些苹果产区,经常发生低温冻害,造成枝条干枯,严重时甚至整株死亡,影响苹果品质和产业的健康发展。20世纪 60 年代中国发现起源于大兴安岭的山定子抗寒性极强,用其做亲本选育了多个抗寒砧木,其中 GM256 和 CX3 是目前报道的我国选育出最抗寒的两个砧木<sup>[31]</sup>。任庆棉<sup>[8]</sup>采用电解质渗出率法对苹果属植物 11 个种 18 个类型进行了耐寒性评价,发现东北山定子和东北黄海棠抗寒性强,分析认为抗寒能力强与东北山定子和东北黄海棠原产地的气候有关,长期受严寒气候环境的影响,逐渐适应了低温环境,因此表现出较强的抗寒性。Mirabdolbaghi 等<sup>[32]</sup>发现 5 种苹果砧木 B9、M9、MM106、M26 和 Azayesh 的耐寒性存在明显差异,B9 耐寒性强。殷丽丽等<sup>[33]</sup>采用低温处理对 4 种苹果砧木 71-3-150、GM256、SH6 和 M9 的抗寒性进行比较分析,发现从俄罗斯引进的矮化砧木 71-3-150 抗寒性最强,其次为 GM256 和 SH6, M9 的抗寒性最差。同时发现低温胁迫下 71-3-150 能维持较高的可溶性蛋白水平及较高的 SOD 和 POD 活性,这可能与其抗寒能力有关。Mirabdolbaghi 等<sup>[32]</sup>将 5 种苹果砧木分别种在不同质地的土壤中,结果发现,苹果砧木 Azayesh 生长在含淤泥 48%、砂 20%、黏土 31% 和石灰 14% 的土壤中抗寒性最好,而 M9 生长在含淤泥 49.2%、砂泥 19.8%、黏土 31% 和石灰 18% 的土壤中抗寒性最好,表明土壤质地也影响苹果砧木的抗寒性。Artlip 等<sup>[34]</sup>将从桃树中分离的 *CBF genes* 转入苹果砧木 M9 后增强了苹果砧木的耐寒性。井俊丽等<sup>[35]</sup>对 9 份苹果种质资源的抗寒性进行了评价,发现新选育的砧木(编号 100 和 147)耐寒性强。

鉴定和挖掘抗寒性强的种质资源是苹果抗寒性砧木育种的前期基础,而探寻适宜快速评价抗寒性

的方法是研究的主要内容之一。在评价抗寒性指标方面,电导率、MDA含量、相对含水量、抗氧化酶活性和脯氨酸含量等指标,被认为与植物的抗寒性密切相关<sup>[8,28,33]</sup>。金明丽等<sup>[36]</sup>研究发现,枝条的电阻抗参数与苹果砧木的抗寒性呈负相关,苹果砧木枝条电阻率及胞外电阻率可以作为评价苹果砧木抗寒性的参数。以上研究结果对在栽培生产中快速评价苹果抗寒性,并及早采取相应的防寒措施具有重要的指导意义。

#### 1.4 耐涝性

水分是影响植物生长和发育的重要因素,然而,土壤水分过多并不利于植株正常生长,甚至会引起涝害发生,涝害已成为威胁苹果生长发育、影响产量及品质提升的主要非生物胁迫之一<sup>[37-39]</sup>。水分过多对植物造成的伤害主要是根部缺氧所致<sup>[40-42]</sup>。植物在低氧条件下,有氧呼吸受到抑制,活性氧等有害物质积累,内源激素代谢紊乱,产生乙醇、乳酸,造成细胞质酸化,最终导致生长受抑,严重情况下导致植物死亡<sup>[37,43-45]</sup>。在实际生产栽培中,夏季和秋季的大量集中降雨和果园排水不良等因素,导致部分苹果园经常积水,苹果树叶片黄化、脱落,树体衰弱,果实品质和产量下降,进而造成严重的经济损失。白团辉等<sup>[10]</sup>采用低氧和盆栽淹水的方法评价了12种苹果砧木的耐涝性,发现平邑甜茶耐涝,而新疆野苹果和变叶海棠不耐涝。生利霞等<sup>[38]</sup>研究表明,平邑甜茶在低氧条件下植株生长受到抑制,根系呼吸速率也受到抑制,并且发现溶氧浓度越低,抑制越明显。Bai等<sup>[43]</sup>研究表明,耐低氧的平邑甜茶根系形态保持较好且在根的基部长出许多新根,而新疆野苹果没有出现此现象。这表明低氧耐性较强的平邑甜茶能够通过维持较高的光合性能来适应低氧逆境,这也正是平邑甜茶比较耐低氧的原因。

#### 1.5 耐缺素

苹果砧木负责从土壤中吸收水分和矿质元素,并将其运输至地上部。因此,砧木直接影响苹果树体的营养水平和正常的生长发育,林冰冰等<sup>[15]</sup>对苹果砧木资源的耐缺铁性进行了评价,发现不同种和生态型耐缺铁性表现出极显著的差异。小金海棠具有较强的稳定的耐缺铁能力,八棱海棠和平邑甜茶抗缺铁能力中等,而山定子抗缺铁能力差。李振侠等<sup>[46]</sup>研究发现缺铁胁迫下两种苹果砧木SH40和八棱海棠的根系分泌有机酸种类相同,但总量有显著

差异。Zhu等<sup>[47]</sup>开发了与小金海棠耐缺铁相关的分子标记,对杂交后代进行鉴定,准确率达到85%以上。刘飞等<sup>[48]</sup>比较了4种苹果砧木的耐缺锌能力,发现小金海棠耐低锌,而山定子对低锌胁迫敏感。王金花等<sup>[49]</sup>比较研究了两种苹果砧木小金海棠和平邑甜茶对缺锌胁迫响应的差异机制,发现缺锌胁迫下小金海棠的抗氧化能力强,对缺锌有较强的抵御和耐受能力。

### 2 苹果矮化砧木资源国内外研究进展及利用

#### 2.1 我国苹果矮化砧木研究进展及利用

矮砧栽培是我国苹果发展的必然趋势,与乔化栽培相比,具有树体矮化、成花早、便于管理等优点<sup>[50-52]</sup>。我国在苹果矮化资源的挖掘及砧木的选育方面起步较晚,目前选育的矮化苹果砧木品种还比较少。SH系是以矮化苹果资源河南武乡海棠和国光为亲本,选育的矮化苹果砧木,如SH6、SH38、SH40。经过多年的推广和应用表明,SH系具有矮化、抗旱、栽植后易成花、结果早等优点,但其抗寒性差,在我国北方地区推广受到限制<sup>[50]</sup>。其他研究单位用引进的苹果矮化砧木M系与我国苹果矮化资源进行杂交,选育出多个矮化苹果砧木品种,包括辽砧系列、GM256、青砧系列、77-34、63-2-19等<sup>[53]</sup>,在我国部分苹果产区推广应用。目前我国苹果生产中应用的矮化砧木主要有M9T337、M26、B9、SH系、GM256等。

秦立者等<sup>[54]</sup>对乔化苹果砧木八棱海棠、半矮化砧木SH3和SH37、矮化砧木SH38、M26和B9及极矮化砧木P22的叶片进行了细胞结构研究,发现苹果砧木的矮化程度越高,叶片栅栏组织越厚。研究表明,植物叶片栅栏组织的厚度、紧密度和疏松度等指标与植物抗寒性密切相关<sup>[55]</sup>。罗静等<sup>[56]</sup>发现以M9和M26矮化中间砧嫁接的长富2号,其净光合速率显著高于以八棱海棠为砧木的苹果树,而气孔导度和蒸腾速率较低,表明矮化中间砧的苹果树光合调节能力强,具有较高的净光合速率。姜志昂等<sup>[57]</sup>对苹果矮化砧木M26、SH28和SH40及嫁接品种嘎拉进行了分析,发现ABA合成基因MdNCED1的表达量与3种砧木嫁接树的矮化程度呈正相关。Zhou等<sup>[58]</sup>通过对B9、G24、M26、SH1、SH6和SH40共6种矮化砧木在高温胁迫下探究生理和基因水平上的变化,发现SH系列砧木耐热性最强,M26的适应能力

最低,G24的恢复能力较高。

## 2.2 国外苹果矮化砧木研究进展及利用

自 19 世纪英国首次报告苹果矮化砧木以来,各个国家都很重视苹果矮化砧木的选育工作,也选育出了一些优良的矮化苹果砧木。如英国的 M 系和 MM 系<sup>[52, 59-60]</sup>,美国的 G 系和 CG 系<sup>[25, 61-62]</sup>,苏联的 B 系<sup>[63]</sup>,日本的 JM 系<sup>[64]</sup>,加拿大的 O 系<sup>[65-66]</sup>和波的 P 系<sup>[67-68]</sup>。美国从 1968 年开始对苹果种质资源进行了广泛评价和筛选,并将苹果砧木育种目标定为矮化、抗火疫病、抗苹果绵蚜、抗重茬、早产丰产等<sup>[67]</sup>。经过连续多年常规杂交,多层次的评价与筛选,最终成功选育出了 14 个广泛推广应用的苹果砧木品种,包括 1 个极矮化砧木(G65)、5 个矮化砧木(G16、G41、G214、G814、G213)、8 个半矮化砧木(G30、G11、G202、G935、G969、G210、G890、G222)<sup>[69]</sup>。

目前,M9 系列中以 M9-T337 应用最为广泛,M9-T337 是荷兰从 M 系中选育出的苹果矮化砧木,用其嫁接的苹果树树体生长矮小,易成花,结果早,且丰产性好<sup>[70]</sup>。由于 M 系砧木抗寒性稍差,苏联选择用抗寒资源与 M 系砧木进行杂交,选育了抗寒性极强的 B 系列矮化砧木,其中 B9 砧木矮化、抗寒性强,且其嫁接的苹果树结果早、丰产、固地性强、能抗 -12 °C 的低温,是推广应用较广的抗寒矮化砧木之一<sup>[71]</sup>。美国康奈尔大学利用 M27、M26、Robusta5 和 Ottawa3 做亲本培育了 G 系砧木,其中 G16、G41 和 G935 矮化且抗苹果再植病<sup>[72-73]</sup>。

## 3 展 望

### 3.1 加强野生苹果种质资源评价与优异基因的挖掘与利用

我国拥有丰富的苹果种质资源,已鉴定出了抗旱种质资源新疆野苹果、楸子,抗寒资源山定子,耐缺铁的小金海棠,矮化资源河南海棠、崂山柰子,无融合生殖资源平邑甜茶、变叶海棠等。但目前仅对部分苹果种质资源进行了鉴定与评价,一些资源还有待鉴定与评价。苹果遗传背景复杂,杂合度高、童期长、个体差异大,精准鉴定与评价比较困难。此外,鉴定与评价方法和技术以传统的形态学观察和生理生化分析为主,重要农艺性状的遗传规律及优异基因的定位与挖掘等研究与其他农作物相比仍有较大差距。因此,应提升苹果种质资源的鉴定与评价水平,加快优异基因的挖掘与利用,为优良苹果砧

木的创制提供优异的基因资源。

### 3.2 创制抗逆和省力化栽培的苹果砧木是将来的育种目标

长期以来,我国苹果产区主要以新疆野苹果、八棱海棠、山定子、平邑甜茶和楸子等作为砧木。虽然新疆野苹果、楸子等抗旱性强,但乔化。平邑甜茶具有无融合生殖特性,但抗旱性差且乔化,且以种子播种的实生苗为砧木,接穗品种存在结果晚等问题。当前缺少抗性强、矮化等综合性状优良的苹果砧木品种。在过去的 30 年中,全球苹果的栽培模式发生了较大变化,由稀植大冠形向矮砧小冠形发展,栽培管理由费时费工向省力化发展。目前,美国、意大利和新西兰等国家苹果矮砧密植栽培占其栽培总面积的 70% 以上<sup>[74]</sup>,而我国仍有 80% 的苹果为乔砧稀植栽培<sup>[75]</sup>,此栽培模式的苹果,树冠大、易密闭、光照不良、品质差,且栽培管理成本高,其中劳动力成本已占苹果生产总成本的 60% 以上。因此,在新形势下,如何培育和创制抗逆和省力化栽培管理的苹果砧木,是将来苹果砧木育种的目标。

### 3.3 利用现代生物技术助力对苹果砧木新品种的选育

苹果砧木培育需要经过长期、系统的鉴定与评价方可推广应用。因此,苹果砧木育种及评价工作比接穗品种的难度更大,周期更长。随着分子生物学和基因组学的快速发展,已经对部分苹果品种进行了全基因组测序,构建了完善的苹果数据库,为优异资源和基因的挖掘、重要基因的克隆和重要性状分子标记的开发提供了坚实的基础。同时,利用基因工程技术和分子辅助育种手段,将特定基因转入苹果砧木的细胞或组织中,有目的地改变性状,培育出抗逆、矮化和无融合生殖的优良砧木已成为可能。

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